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BIODIVERSITY RESEARCH

Seedling establishment of Asteraceae forbs along altitudinal gradients: a comparison of transplant experiments in the native and introduced ranges

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ABSTRACT

Aim Since ecological and evolutionary context changes when a plant species is introduced to a new area, it can be assumed that responses of alien plants to changing conditions along environmental gradients differ from those in their native range. Even if seed availability is not limited, the distribution of alien plants along such a gradient might still be restricted by their ability to germinate and establish as seedlings. In the present study, we aim at testing what factors promote or limit plant invasions during early establishment by using altitude as a model gradient.

Location Altitudinal gradients in the Wallowa Mountains (Oregon, USA) and the Swiss Alps (Valais, Switzerland).

Methods In transplant experiments along altitudinal gradients, we investigated the early establishment success of eight invasive alien Asteraceae species in their native and introduced ranges in the Wallowa Mountains and the Swiss Alps.

Results Seedling recruitment was not restricted to relatively lower altitudes in the introduced range. In addition, we found no evidence for genetic adaptation along the altitudinal gradient in the introduced range, highlighting the importance of phenotypic flexibility for invasions. Furthermore, seedling recruitment was only enhanced by disturbance in the native range where vegetation was comparably dense but not in the introduced range. However, plant development was strongly delayed in the introduced range, probably due to low seasonal water availability.

Main Conclusions We conclude that introduced plants, due to their ability to tolerate a wide range of environmental conditions, are not necessarily more restricted in their altitudinal limits than they are in their native range. Furthermore, due to other interacting factors (e.g. different competition situations among ranges), attempts to predict distributions of alien plants in the introduced range that are based on their distributions in the native range may be misleading.

Keywords
Altitude, biological invasions, disturbance, environmental gradients, plant invasions, roadsides, transplant experiment.

INTRODUCTION

Most plant species introduced into regions with strong environmental gradients, e.g. high mountains, reach their distributional limit at some point along these gradients (Becker *et al*., 2005). To understand the factors that promote or limit a plant invasion, it is therefore important to investigate species traits and responses to varying growth conditions across the entire introduced range and not only where the species is most successful (Rice & Mack, 1991; Kitayama & Mueller-Dombois, 1995; Kollmann & Banuelos, 2004; Dietz & Edwards, 2006).

Important factors restricting spread into less favourable regions include changing abiotic or biotic conditions, dispersal constraints (reduced propagule pressure) and limits to the species' ability to cope with changing conditions by genetic adaptation or phenotypic flexibility. If there is a dynamic invasion

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front, the role played by these factors in limiting invasion is likely to be most apparent near the margins of the distribution range of the species (Antonovics, 1976; Dietz & Edwards, 2006; Parmesan, 2006). Hence, investigations into the mechanisms driving or constraining plant invasions along extensive environmental gradients may improve our ability to predict the spread of introduced plant species, especially in the face of climate change. In the case of high mountains, adverse abiotic conditions and low availability of propagules are likely to be important factors limiting invasion towards higher altitudes. In particular, more limiting growth conditions (e.g. cooler temperatures and shorter growing seasons) at higher altitudes in temperate mountains decrease the chances of plant establishment (Körner, 1999). Accordingly, the most sensitive state in a plant's life cycle, especially at high altitudes, is the emergence and establishment of seedlings (Körner, 1999). It is less clear, however, how interactions with other plants might influence seedling emergence and establishment of introduced plants; while the germination of seedlings may be favoured by open conditions (Wester & Juvik, 1983), their subsequent survival at high altitudes may be facilitated by the presence of neighbouring plants (Callaway & Walker, 1997; Choler *et al.*, 2001; Pugnaire & Luque, 2001). Successful seedling establishment of introduced plant species at higher altitudes may therefore be the most crucial event for pushing the range limit of a plant invasion along such an environmental gradient.

So far, most studies of the factors influencing the distribution of introduced plant species in mountains have relied on observational data (Williams *et al.*, 1995; Cavieres *et al.*, 2005). We know of only one study – by Paiaro *et al.* (2007) – that used an experimental approach to investigate constraints of seedling emergence and establishment of introduced plant species along broad altitudinal gradients, and that only in the introduced range. This is a pity, since experiments that translocate propagules or seedlings along environmental gradients are a powerful way of testing whether seedling establishment at or beyond the range margin is constrained by abiotic or biotic conditions or by low propagule pressure. If the current boundaries of a species are set mainly by abiotic or biotic factors, we would expect seedling establishment to be limited close to the species' current altitude of occurrence. In contrast, if they are mainly limited by the availability of propagules, we would expect seedling establishment to be successful at or beyond the species' present distribution limits. In addition, transplant experiments may be used to investigate whether the species shows local adaptation, or copes with changing conditions towards its distribution limits through tolerance of a wide range of conditions (phenotypic flexibility). If local adaptation is important (and provided the species' range is not strongly limited by the supply of propagules), we might expect lower altitudinal distribution limits in the introduced range because there has been insufficient time to adapt to conditions in the new area. Alternatively, if the species exhibits high phenotypic flexibility there may be no difference in the highest altitudes reached by native and introduced populations.

We chose two temperate mountain systems, the Valais region in the Swiss Alps and the Wallowa Mountains in the northwestern USA, in which to study the factors affecting altitudinal limits of native and introduced plant populations. The two areas are climatically comparable and are easily accessible up to (sub-)alpine altitudes. Furthermore, both areas share several species of Asteraceae, these being native in one area and introduced in the other. Hence, the two areas were intended as reciprocal study systems for comparisons of seedling emergence and establishment in Asteraceae forbs along altitudinal gradients in the native and the introduced ranges.

To determine the factors influencing seedling establishment of introduced species along altitudinal gradients, we focused on the following questions: (1) To what degree are present altitudinal limits of the species determined by either low seed availability or unsuitable abiotic conditions for germination and establishment? (2) Does the effect of vegetation cover on seedling establishment vary with altitude (e.g. negative interactions predominating at lower altitudes and positive interactions predominating at higher altitudes)? (3) Is seedling establishment more restricted to lower altitudes in the introduced range than in the native range, and if so, is this due to maladaptation in the introduced range?

To investigate these questions, we transplanted seed of eight common Asteraceae species from low and high elevations along altitudinal gradients in the native and the introduced range (within-range transplantations). At each altitude, seed was sown into artificially disturbed plots without plant cover, and into the native vegetation matrix along mountain roadsides. Seedling recruitment and seedling development were recorded at monthly intervals.

METHODS

Study areas

The experiments were conducted in the canton Valais in the Swiss Alps (46° N, 7° E) and in the Wallowa Mountains in Eastern Oregon, USA (45° N, 117° W). The two areas have a different geological history but are climatically similar. The Swiss Alps have risen from the collision of the European and the African plate. The soils to the north of the river Rhone in the middle part of the Valais have developed mainly on limestone, whereas soils in the lower and upper Valais have developed on silicate rock (Werner, 1994). In contrast, the Wallowa Mountains, as part of the Blue Mountain range are made up of heterogeneous terrain that was accreted to the continent when the North American plate moved west toward the Pacific. At low altitudes the bedrock consists mainly of sedimentary deposits and at high altitudes mostly of basalt and granite (Alt & Hyndman, 1978).

Both areas are characterized by a temperate, continental climate. In the Valais, mean annual minimum temperature is a little higher, and mean annual maximum temperature a little lower than in the Wallowa Mountains (Table 1), but in both systems mean temperatures decrease similarly with increasing altitude (Fig. 1a). The number of days above a mean temperature of 5 °C is also similar in both regions (Fig. 1b). Precipitation is moderately higher in the Valais than in the Wallowas (Table 1), where most rainfall occurs during the winter months in form of snow (Pohs, 2000).

	Wallowa Mountains (USA)	Valais Alps (Switzerland)
Altitudinal range of roads (m a.s.l.)	~900–2200	~500–2400
Mean annual precipitation (mm)	449*	598†
Mean annual minimum temperature (°C)	–0.3*	3.6†
Mean annual maximum temperature (°C)	15.1*	14.8†

*Average for Cove (1961–1990) and Enterprise (1931–1981), 45° N, 117° W, Oregon, USA (www.wrcc.dri.edu).
†Average for Sion and Visp (1961–1990), 46° N, 7° E, Switzerland (www.meteoschweiz.ch).

Table 1 Geographical and climatic conditions of the study systems. Precipitation, minimum and maximum temperatures were taken from valley level.

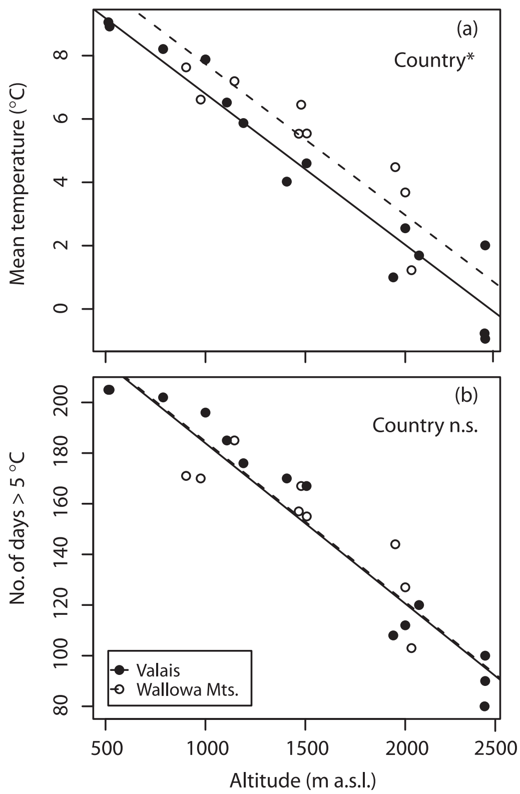

Figure 1 Relationship between altitude and (a) mean temperature (°C) and (b) number of days > 5 °C in the two mountain systems. Valais (Switzerland) data were collected between November 2004 and October 2005 (filled circles, solid line), Wallowa Mountains (USA) data from November 2005–2006 (open circles, dotted line).

In the Valais, the lower elevations up to about 800–900 m are densely populated and used for agriculture, viniculture and industry. At mid- to high elevations, *Picea abies* and *Pinus sylvestris* dominate (~900–2000 m), later joined by *Larix decidua* and *Pinus cembra* (Landolt, 2003). Settlements can be found scattered across the slopes up to the subalpine, and the land is used for haymaking and sheep/cattle grazing, the latter extending to altitudes up to 2200 m. At higher elevations at and above the timberline, anthropogenic influence is mainly restricted to recreational activities (e.g. hiking, skiing).

The Wallowa Mountains have only been exposed to intensive land use since the arrival of European settlers around 1843. The foothills of the Wallowa Mountains are mainly characterized by arid grassland and shrub steppe vegetation (Parks *et al.*, 2005) and are primarily influenced by farming activities and a few settlements. Low to mid-elevations (approximately 900–1600 m) are characterized by relatively open forest dominated by *Pinus ponderosa* and *Pseudotsuga menziesii*. This zone is mostly used for cattle ranching and timber extraction. Above 1600 m, *P. menziesii* and *Larix occidentalis* dominate (Pohs, 2000; Parks *et al.*, 2005), and the timberline is reached at around 2600 m (Pohs, 2000). As in the Valais, high elevations are much less affected by human activities.

Both regions are easily accessible by roads, reaching up to about 2400 m in the Valais and 2100 m in the Wallowa Mountains. Roadsides are highly influenced by human disturbance in both study systems. In the Valais, roads range from small trails to international traffic routes that run along the major valleys and over mountain passes. They are mainly affected by traffic but also by maintenance work and mowing at regular intervals. In the Wallowa Mountains, roads tend to be smaller and more local and mostly do not cross the mountain range. The roadsides are influenced not only by traffic, but also by logging activities and locally by herbicide usage against weeds.

Study species

We selected eight species of Asteraceae forbs for our experiments: four of these are native to North America and were introduced to Europe, and the other four species are native to Europe and introduced to North America (Table 2).

The North American natives are all common weeds of mostly disturbed ground in the Valais region. *Conyza canadensis* (L.) Cronq. (Canadian horseweed) was introduced as early as 1800, whereas *Erigeron annuus* (L.) Pers. (Eastern daisy fleabane), *Matricaria discoidea* DC. (Disc mayweed) and *Solidago canadensis* L. (Canada goldenrod) were introduced after 1900. The first three species are annuals reproducing only from seed, while *Solidago canadensis* is a rhizomatous perennial that also spreads vegetatively. The *Solidago* complex is taxonomically difficult; at the beginning of the study the taxon occurring in the Wallowa

Table 2 Native distribution and life history characterization of the study species.

Species	Origin	Life cycle	Fertilization
Cichorium intybus L.	Europe	Perennial	Outcrossing
Cirsium arvense (L.) Scop.	Eurasia	Perennial	Outcrossing, vegetatively
Cirsium vulgare (Savi) Ten.	Eurasia	(Annual–) biennial	Mixed
Lactuca serriola L.	Eurasia	Annual (–biennial)	Autogamous
Conyza canadensis (L.) Cronq.	N. America	Annual	Mixed
Erigeron annuus (L.) Pers.	N. America	Annual–biennial	Apomictic
Matricaria discoidea DC.	N. America	Annual	Autogamous
Solidago canadensis L./ *S. lepida* (DC.) Cronq.	N. America	Perennial	Outcrossing, vegetatively

Mountains was thought to be *Solidago canadensis* (i.e. the same species as in Europe), but a recent revision describes it as *S. lepida* (Semple & Cook, 2006). However, both species are closely related within the complex, and we have used *S. lepida* for comparison with *Solidago canadensis* in Europe.

The species native to Europe were most likely introduced to the northwestern USA between 1850–1920 during the main settlement period of the area by Europeans (Parker *et al*., 2003). They are considered introduced throughout the USA, and are listed as noxious weeds in some states (USDA, 2007). *Lactuca serriola* L. (prickly lettuce) is a winter annual, *Cirsium vulgare* (Savi) Ten. (bull thistle) a biennial, and *Cichorium intybus* L. (chicory) a short lived perennial species. These species reproduce only by seed. The perennial *Cirsium arvense* L. (Canada thistle) also reproduces vegetatively by lateral roots.

Seed collection

Seeds of all species were collected in both areas in autumn 2004 and in autumn 2005. In each area we sampled from one low and one high altitude site along each of three mountain roads (three replicates). Low origin seeds were collected from populations of the species growing in the foothill area of the two mountain systems. For the high altitude seeds, we collected from the highest populations that were producing seeds. If one population did not provide enough seeds, as was sometimes the case at high altitudes, seeds from neighbouring populations were combined. Depending on the species, population size and seed availability, seeds from 1 to 55 seed families per population were collected and pooled. To avoid the risk of introducing novel genotypes to new areas, seeds were not redistributed among roads.

Experimental design

Seeds of each species were sown into sites along the altitudinal gradient (50–200 seeds depending on the species). These sites were chosen at the lowest possible altitude on each road (F), at the upper altitudinal limit of species occurrence (L, highest seed origin), and above this limit (H, at about 2000 m; Fig. 2). Two further intermediate sites were used above the low altitude (FI) and below the high altitude (LI) site. Where roads or tracks went above 2000 m, additional sites were chosen for about every 200 m of increase in altitude or at the highest altitude accessible. At each of the sites, plots were placed along the roadside, about 1 to 5 m from the edge of the road, preferably into unshaded habitat. For sites F, L and H, four square 1 m^2 plots 0.5 m apart were set out. These were used for a factorial design with 2 seed origins × 2 disturbance treatments. Two plots were used for low origin seed and two for high origin seed. One of the two plots per seed treatment was left undisturbed, whereas the vegetation in the other was removed and the topsoil layer was turned over to prevent re-establishment of the native vegetation prior to sowing. Each plot was further divided into four subplots, each receiving seed of a different species. The FI and HI sites were set up in the same way, but due to limited seed availability of high origin seed, only low origin seed was used in this case (resulting in only two plots per site).

The experiment was set up in both areas in autumn 2004 for the introduced range of each species. In autumn 2005, the experiments were repeated for the native ranges of the species.

Data collection

Numbers of individuals and their life stages were recorded in each plot at monthly intervals during the growing season (May to September) of the year following sowing. Four life stages were distinguished – seedling/vegetative (only leaves present), bolting (development of a shoot), flowering (presence of flower buds and flowers) and fruiting (seeds developed on the plant or presence of empty seed heads). The total numbers of plant individuals were counted each month without distinguishing between newly germinated seedlings and older plants (seedlings were not marked individually to avoid drawing attention to the plots).

Statistical analyses

All statistical analyses were performed with R (version 2.3.0 for Mac OS X, The R Foundation for Statistical Computing). Analyses were performed on the cumulative number of seedlings recruited over all months of the growing season (seedlings were counted monthly between May and September). The responses of the study species to altitude and to treatment differences as

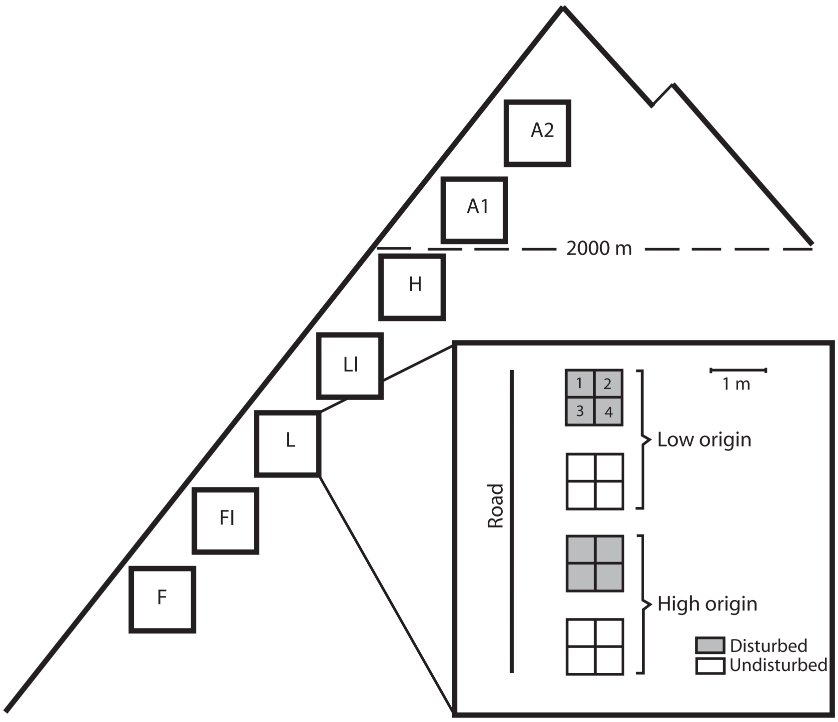

Figure 2 Experimental set-up along an altitudinal gradient with main sites at the foothill (F), the species altitudinal limit (L), at high altitude at 2000 m (H) and intermediate sites between F and L (FI) and L and H (LI). One or two additional sites were placed at 2200 m with every 2400 m (A1 and A2) if possible. The numbers 1 to 4 denote the different species used per plot.

well as their interaction (altitude × treatment) were analysed using linear regression models for each species separately. As the relationship between number of individuals per plot and altitude was clearly different in the lower altitudinal zone from that in the upper altitudinal zone in disturbed plots in Switzerland, we analysed these data also with two-part linear regressions (Toms & Lesperance, 2003). This procedure is based on the assumption that the relationship between X (altitude) and Y (number of individuals) consists of two linear sections characterized by different slopes. The breakpoint, where the regression lines meet, was identified by calculating multiple regressions for every 50 m of increase in altitude (from 500–2400 m) and by estimating their optimality for fitting the data; the point with the least error distribution was taken as the breakpoint. Subsequently, two regression models were calculated, one for below (t_{below}) and one for above the breakpoint (t_{above}) to analyse if there was a significant change at that point, and if the regression below is significantly different from zero.

We tested for a possible effect of high versus low seed origin using the data for two of the species (*C. arvense* and *C. vulgare*) in the native and introduced ranges. An analysis of variance (ANOVA) including two-way interactions was used to test the effect of altitude, altitude origin, species, treatment and road on seedling numbers for *C. arvense* and *C. vulgare*.

To make seedling population size comparable between species (different seed densities were sown depending on the amount of seed a species yielded), data were calculated on the basis of 100 seeds per species and plot. All models were checked for normality of errors and plant numbers were log-transformed to meet this assumption.

RESULTS

General patterns of seedling emergence – North American species

In most of the Swiss experimental plots hardly any seedlings of the North American species emerged. If seedlings emerged, they did so in the disturbed plots and often in quite high numbers. For example, in June 2005, 158 *M discoidea*, 39 *C. canadensis* and 22 *S canadensis* seedlings were present in a disturbed plot at 1200 m into which 200 seeds were sown the year before, but no seedlings could be observed in most of the other plots along all three roads. In the Wallowas, a higher number of seeds of the North American species germinated along the gradient and seedlings were mostly present at lower and intermediate altitudes, but hardly any of them survived the summer. Many seedlings did not survive long enough to be unambiguously assigned to a species. Seedling numbers in a plot were low and variable. In June, for example, the plots harboured between zero and 34 seedlings. In the Wallowas, seedling establishment was not as restricted to disturbed ground as in the Swiss Alps. The overall low seedling emergence of the North American species in both countries made a detailed statistical analysis of the data impossible.

General patterns of seedling emergence – European species

In both study areas, some seeds of all European species germinated along the whole altitudinal gradient, from the valley bottom up to the highest experimental plots at 2150 m in the Wallowa

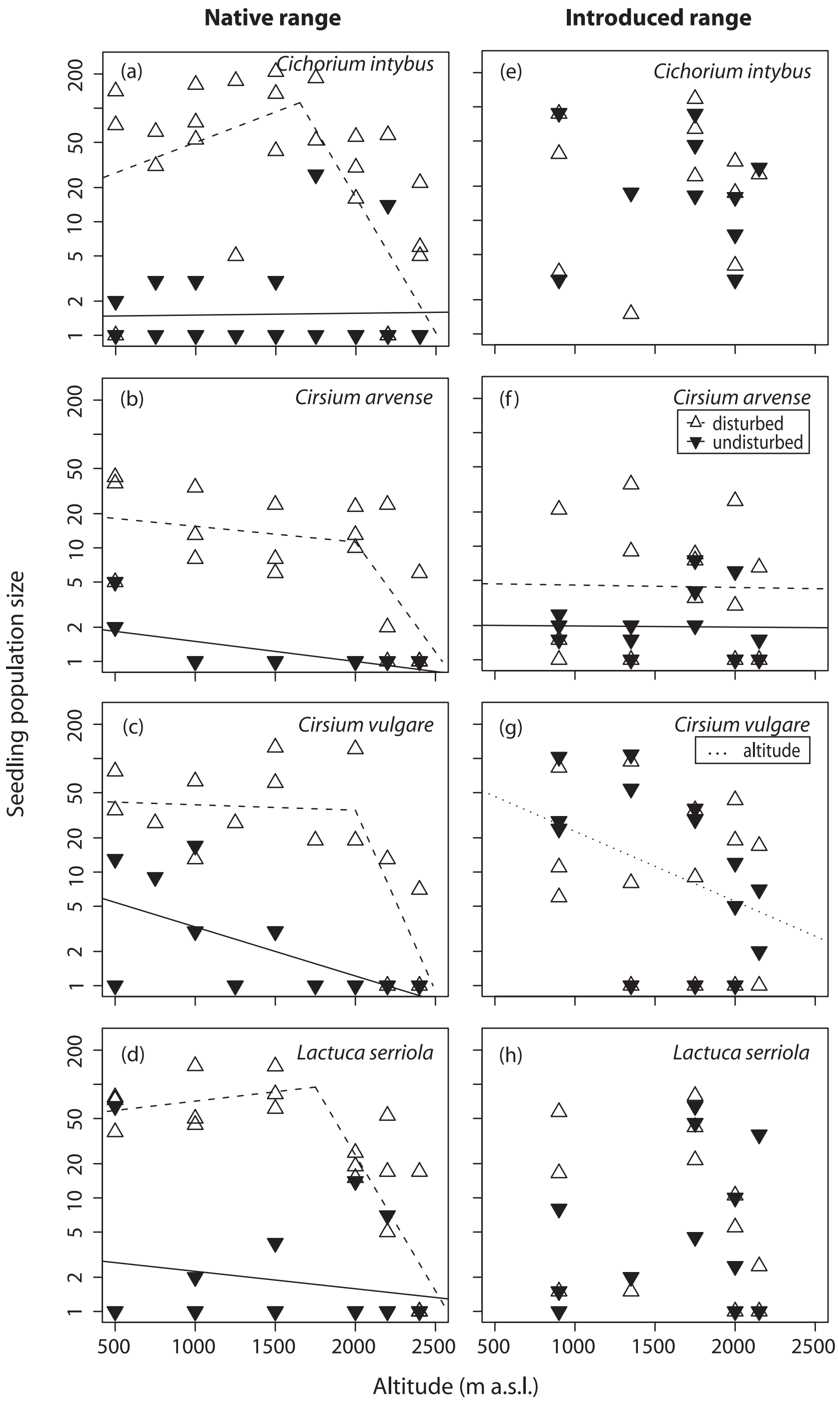

Figure 3 Species-specific relationship between altitude and seedling population size for low origin seed under disturbed and undisturbed conditions in the native Swiss Alps (a–d) and the introduced Wallowa Mountain range (e–h). Note the log scale of the *y*-axis. For statistical analyses see Tables 3 and 4.

Mountains (introduced range) and 2400 m in the Valais (native range). However, establishment of seedlings generally declined with altitude, with the patterns differing between the two study systems (Fig. 3, Table 3). In the native range of the species (Valais), the decline was relatively strong, with numbers of individuals decreasing from a mean across all species and treatments of 30 plants at the lowest sites to three plants at the highest sites (Fig. 3a–d). This decrease of seedling numbers with altitude was significant ($P < 0.01$) for all species except *C. intybus.* In the introduced range, numbers of individuals per site declined less strongly, from an average of 25 seedlings at the lowest altitude to eight per site at the highest (across species and treatments, Fig. 3e–h). Treating the species individually, this decline was only significant for *C. vulgare* ($P < 0.05$).

The effect of disturbance on seedling establishment differed strongly between the native and introduced ranges (Fig. 3, Table 3). Under disturbed conditions in the native range, seedlings of all species established well up to moderately high altitudes (e.g. at 1500 m on average 80 plants per site over all species). In contrast, under undisturbed conditions seedling establishment was generally much lower, and hardly any seedlings emerged at higher altitudes (at 1500 m an average of

Table 3 Results of linear regression analyses of the relationship between seedling population size and altitude in disturbed versus undisturbed plots (only for low origin seed) in the native Swiss Alps (Valais) and the introduced Wallowa Mountain range. Shown are degrees of freedom (d.f.), sums of squares (SS), F-values (F) and significance values (P).

	Native range				Introduced range			
	d.f.	SS	F	P	d.f.	SS	F	P
Cichorium intybus								
Altitude (A)	1	3.5	2	NS	1	< 0.1	0.001	NS
Treatment (T)	1	101	57	< 0.001	1	0.1	0.03	NS
A:T	1	3.7	2.1	NS	1	0.15	0.07	NS
Residuals	43	76			17	32.9		
Cirsium arvense								
Altitude (A)	1	7.7	12.2	< 0.01	1	< 0.1	< 0.1	NS
Treatment (T)	1	33.3	53.1	< 0.001	1	4.6	4.1	0.05
A:T	1	1.6	2.5	NS	1	< 0.1	< 0.1	NS
Residuals	31	19.4			24	26.9		
Cirsium vulgare								
Altitude (A)	1	15	13.2	< 0.01	1	11.3	4.5	< 0.05
Treatment (T)	1	43.2	38	< 0.001	1	0.3	0.1	NS
A:T	1	0.2	0.2	NS	1	1.9	0.75	NS
Residuals	27	30.7			24	59.6		
Lactuca serriola								
Altitude (A)	1	12.8	9.6	< 0.01	1	< 0.1	< 0.1	NS
Treatment (T)	1	63.3	47.3	< 0.001	1	0.8	0.3	NS
A:T	1	4.6	3.4	0.07	1	3.4	1.3	NS
Residuals	32	42.8			20	52.1		

NS, not significant.

0.8 plants per plot over all species; Fig. 3a–d). This difference between treatments was found to be highly significant for all species in the native range ($P < 0.001$). In addition, very few seedlings survived the whole season in the undisturbed plots, and these mainly in plots where the vegetation was sparse. In the introduced range, the effect of the disturbance treatment was less clear, with disturbed plots containing only slightly more seedlings than undisturbed plots (overall averages of 26 seedlings in disturbed versus 23 in undisturbed plots; Fig. 3e–h). Only for *C. arvense* was seedling establishment noticeably increased in the disturbed plots (Fig. 3f, $P = 0.05$).

In the native range of the species, the numbers of plants in the disturbed plots were relatively constant up to 1650 to 2000 m, depending on the species, but decreased strongly at higher altitudes ($P \leq 0.01$, Fig. 3a–d, Tables 3 and 4). For *C. intybus* and *L. serriola*, seedling numbers declined from approximately 100 seedlings per plot to almost zero between about 1700 and 2400 m. *C. arvense* and *C. vulgare* still produced on average about 14 and 33 plants per plot at about 2000 m but hardly any seedlings established at 2400 m. In the introduced range, there were no significant declines in numbers of seedlings with altitude in either disturbed or undisturbed plots (with on average 7 to 10 seedlings per plot).

Effects of seed origin – European species

In the native area under disturbed conditions, seed of low origin produced more seedlings at low and medium altitudes than seed of high origin; in contrast, seedling establishment from high origin seed was relatively greater at high altitudes (Fig. 4a–b). In the introduced area, the numbers of seedlings per plot appeared to be less dependent on seed origin, though more seedlings established from seed of high origin than of low origin in the disturbed plots at intermediate altitudes (Fig. 4c–d). ANOVA (Table 5), however, provides no statistical support for an effect of seed origin on establishment success in both the native and the

Table 4 Results of the two-part linear regressions for the relationship between altitude and seedling population size in the native range (Swiss Alps, disturbed plots only). Shown are the altitude of the breakpoints, the t-values and the significance levels for the regression below the breakpoint (t_{below}) and the t-value and the significance level for the regression above the breakpoint (t_{above}). r^2 denotes the explained variance of the whole model. See Fig. 3(a)–(d). $P < 0.001$ ***, $P < 0.01$**, $P < 0.05$*

	Breakpoint (m a.s.l.)	t_{below}	t_{above}	r^2
Cichorium intybus	1650	1.4	–2.6*	0.33**
Cirsium arvense	2000	–0.7	–2.1*	0.49**
Cirsium vulgare	2000	–0.2	–2.8*	0.59**
Lactuca serriola	1750	0.6	–3.4**	0.69***

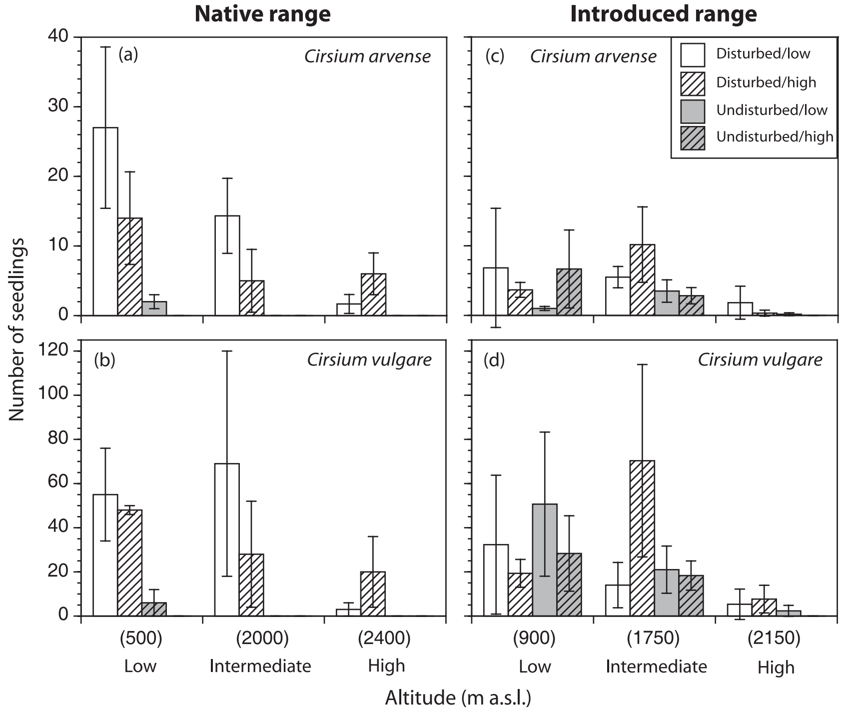

Figure 4 Number of *Cirsium arvense* and *C. vulgare* seedlings in the transplant plots at low, intermediate and high altitudes in the native Swiss Alps (a–b) and the introduced range in the Wallowa Mountains (c–d). Shown are data with standard errors for the different treatments (disturbed/undisturbed plots) and seed origins (low/high altitude). The respective altitudes are given in parentheses. The corresponding statistical parameters for Fig. 4 are shown in Table 5.

Table 5 Results of an analysis of variance (ANOVA) on seedling number for three sites that received high and low origin seed in the native Valais (Fig. 4a–b) and introduced Wallowa Mountain range (Fig. 4c–d). Effects of altitude, altitude origin, species, treatment and road and their interactions were tested combined for *Cirsium arvense* and *C. vulgare* (only significant interactions were included in the table).

	Native range					Introduced range				
	d.f.	SS	MS	*F*	*P*	d.f.	SS	MS	*F*	*P*
Altitude (A)	2	14.62	7.31	9.89	< 0.001	2	45.1	22.5	23.7	< 0.001
Altitude origin (AO)	1	1.01	1.01	1.37	NS	1	0.4	0.4	0.4	NS
Species (S)	1	4.82	4.82	6.52	< 0.05	1	23.9	23.9	25.1	< 0.001
Treatment (T)	1	70.17	70.17	94.97	< 0.001	1	1.4	1.4	1.5	NS
Road (R)	2	5.71	2.85	3.86	< 0.05	2	9.7	4.8	5.1	< 0.01
A:S	–	–	–	–	–	1	6.7	6.7	3.5	< 0.05
S:T	1	4.06	4.06	5.49	< 0.05	–	–	–	–	–
Residuals	51	37.68	0.74			63	59.0	0.9		

d.f., degrees of freedom; SS, sums of squares; MS, mean squares; *F*, *F*-values.

introduced range, nor for any interaction between seed origin and disturbance.

Plant development – European species

The subsequent fate of seedlings differed considerably between the native and introduced areas (Fig. 5). Seedlings of most species in the introduced range survived until the end of the season up to 2000 m, whereas in the native range they survived up to 2200–2400 m. However, in the native range, seedlings survived only in fairly small numbers at high altitudes, except for one site that provided unusually moist and warm conditions. In the introduced range, all species except *L. serriola* remained at the seedling or vegetative stage throughout the study period, whereas in the native range *C. arvense* produced shoots up to 2000 m and *C. intybus* set seed up to 1500 m (Fig. 5). Only *L. serriola* reached reproductive maturity at higher altitudes in both ranges, producing seed up to 1500 m in both ranges, and buds or flowers up to 1800 m and 2000 m in the introduced and native ranges, respectively.

DISCUSSION

General patterns of seedling emergence along the altitudinal gradient

Since very low and inconsistent seedling emergence of the North American species in both countries made a detailed statistical

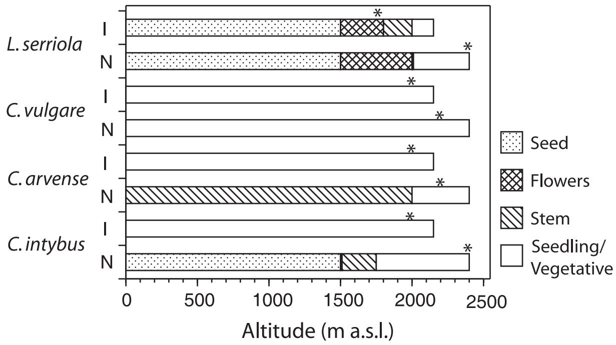

Figure 5 Maximum altitude (m a.s.l.) of different life cycle stages developed in the study species (*Cichorium intybus*, *Cirsium arvense*, *Cirsium vulgare* and *Lactuca serriola*) within one growing season in the native (N) and introduced (I) ranges. Data shown are for all seed origins and treatments combined. The highest sites investigated were at 2150 m in the Wallowa Mountains and 2400 m a.s.l. in the Valais, respectively. Asterisks indicate the highest altitudes for the study species and the respective regions that were reported previously (J. Alexander, personal communication).

analysis of the data impossible, the discussion focuses on the European species.

Most species were able to germinate along the entire altitudinal gradients within both the native range in the Valais (highest site 2400 m) and in the Wallowa Mountains (highest site 2150 m). As the highest plots were above the present altitudinal limits of all species, it seems that the ecological niches for seedling emergence along the altitudinal gradient are larger than those for development of reproducing individuals. Therefore, either the realized niche for successful site colonization of the species (including all life stages) is more constrained than that of seedling emergence, or low propagule pressure limits the present occurrence of the species towards higher altitudes. However, because seedling establishment was possible above current maximum altitudes in both the native and the introduced ranges, there seems no need to invoke propagule pressure to explain the 'out of range' seedling establishment in the introduced area. Other experimental studies also support the finding that introduced species are not limited to lower elevations. Paiaro *et al.* (2007), for example, found *Melilotus alba* and *C. vulgare* seedling recruitment in Argentinean mountain grasslands up to 2200 m, with *C. vulgare* recruitment even increasing with altitude. They related the successful establishment of seedlings over the whole gradient to a close matching of climate between high altitude areas in Argentina and the species' native areas. In our case this effect of high altitudes in the introduced range matching with low altitudes in the native range is less significant, as the study systems were chosen to be climatically similar over the whole investigated gradient.

Seedling emergence in the native range was relatively uniform up to 1600–2000 m a.s.l. in the disturbed plots, but decreased rapidly at higher altitudes. This response suggests that seedling emergence can occur across a relatively wide climatic gradient, but that establishment is strongly reduced if climatic harshness surpasses a certain threshold where physiological requirements (e.g. in terms of soil temperature, moisture and light quality) are not met (Baskin & Baskin, 1989). A similar observation was made by Hügin (1995), who demonstrated that the natural limits of altitudinal distributions even for strict synanthropic species often depend on climate. Stronger competition can be ruled out as a factor reducing seedling emergence at high altitudes in the disturbed plots because recolonization of the disturbed plots by the surrounding vegetation or regenerating plant fragments was mainly limited to plots at low altitudes. In the native range, where the existing vegetation was very dense, seedling emergence was consistently lower in undisturbed plots compared to the disturbed plots and hardly any seedlings emerged in undisturbed, vegetated plots at higher altitude. This indicates that competition by the existing vegetation reduced seedling establishment considerably, especially at higher altitudes. We have no reason to suppose that the same effects of competition do not also apply in the introduced area, but any such effects were partly obscured because the roadside vegetation in the Wallowa Mountains was more open, and so the undisturbed and disturbed treatments did not differ greatly. In general, however, seedling establishment of the species under unmanipulated conditions was considerably higher in the introduced range than in the native range, especially at intermediate altitudes. Hence, it seems that in this altitudinal zone where growth is not strongly limited by low temperatures, release from stress (e.g. drought, competition) is particularly beneficial for seedling establishment in the introduced area.

Our results suggest that the presence of vegetation increasingly restricts the establishment of introduced plants at higher altitudes. Thus, there is no indication that establishment was facilitated by established plants, as has been reported for introduced species in the Chilean Andes (Cavieres *et al.*, 2005) and for native plants in the alpine zone (Callaway *et al.*, 2002). However, in the study by Callaway *et al.* (2002), facilitation was demonstrated by removing neighbours from the vicinity of established plants. It may be that such positive interactions only predominate at later growth stages, and that competitive interactions are more important during establishment.

Establishment and growth

More seedlings at high altitudes survived until the end of the season in the native than in the introduced range, with survival being highest on warm, south-facing sites that were not moisture limited. At higher altitudes, the three monocarpic or polycarpic perennial species either produced no seed in the first year (*Cichorium intybus*) or did not develop reproductive structures at all (*Cirsium arvense* and *C. vulgare*). For these species we are therefore unable to determine the maximum altitudes at which seed production can occur. However, in all three species plant development advanced less in the introduced range than at similar altitudes in the native range. This could be because conditions were generally less favourable for plant growth, or may reflect a lack of adaptation of these plant populations to conditions in the Wallowa Mountains. Specific conditions limiting growth in the

Wallowa Mountains probably include nutrient-poor soils at mid- and high altitudes and periodic water stress, as most of the annual precipitation in the Wallowas falls in winter (Pohs, 2000). It is also possible that the delayed development of plants in the introduced range reflects a shift in life cycle from monocarpy to polycarpy. Such a shift has been noted in several invasive plants and has been related to release from specialist herbivores (Müller-Schärer & Steinger, 2004; Müller-Schärer *et al.*, 2004; and references therein).

Being a true annual, *Lactuca serriola* was the only species that entered the reproductive state, up to intermediate altitudes, within one growth period in both ranges. Surprisingly, and in contrast to the other species, the maximum altitudes where seed production or flowering was reached were very similar between ranges. It seems that this ruderal plant species is better able to cope with varying growth conditions along environmental gradients. The results also suggest that in years favourable for plant growth, the species might produce seed up to about 2000 m not only in the native but also in the introduced range. As the highest occurrences of the species outside of the experimental plots corresponded approximately to the maximum altitudes of seed production in both ranges, *L. serriola* might have reached its stable altitudinal limits under the current climatic conditions in both ranges at about 1500–1650 m.

Altitudinal origin

In contrast to the introduced range, where seedling origin did not affect recruitment differently at low and high altitudes, there was evidence for genetic differentiation between low and high altitude seeds in the native range. Although this differentiation did not compensate the greatly limiting effects that led to the strong decrease identified above 1650–2000 m, stronger adaptation to local conditions might explain the higher overall recruitment success in the native range. In contrast, in the introduced range, local adaptation could have been restricted, either because of the lack of suitable genetic variation, or because there has been insufficient time since introduction (or both). As all the species are common in the native range and are likely to have been introduced many times in grain or seed mixtures, lack of genetic variation seems unlikely. In a related study by Alexander (2007) genetic variation in *L. serriola* was even shown to be higher in the introduced range than in the native range and adaptive population differentiation along latitudinal gradients has been found to occur rapidly for other introduced species (*Solidago altissima* and *S. gigantea*; Weber & Schmid, 1998).

Implications for plant invasions along the altitudinal gradient

Our transplant experiments demonstrate that the occurrence of plant species along extensive altitudinal gradients in temperate mountains, at least in the recruitment phase, is not necessarily more constrained in the introduced area than in the native area. Rapid adaptation (Maron *et al.*, 2004) to constraints important in the recruitment phase along extensive altitudinal gradients is unlikely to be a major reason for this unexpected similarity between the native and the introduced ranges, because germination success and early seedling establishment was mostly independent of the altitudinal origin of the seed material. Rather, high phenotypic flexibility or a high genetic diversity within species due to multiple introductions (Sakai *et al.*, 2001) seems to have allowed the species to cover similar ranges in both systems.

In this respect, our study adds to a large body of evidence suggesting that successful spread of introduced plants in heterogeneous environments is related more often than not to high variation potential in the species' responses (Baker, 1965; Williams *et al.*, 1995; Parker *et al.*, 2003). This variation is more likely to be imported to the new area than newly attained.

Overall, our results demonstrate that over extensive environmental (altitudinal) gradients, more stressful abiotic conditions need not be important constraints for the recruitment phase of an invasion by an alien plant. More crucial is whether propagules reach those altitudes.

Assuming that propagule pressure is not limiting, then partial escape from some factor restricting population growth in the native area could explain the greater abundance of the species in the introduced area. In our case, the constraining factor appears to be competition with established vegetation, which is much stronger in the native range and affects plants most strongly in the recruitment phase. The stronger decrease in recruitment with altitude in undisturbed versus disturbed plots demonstrates that such constraints might also affect the distribution of alien species along altitudinal gradients. Although the fundamental niche of the species might be the same, these differences in constraining factors could lead to differences in the realized niche between ranges. This could seriously reduce our ability to predict a species' (altitudinal) presence in the introduced range on the basis of its native range distribution (Peterson, 2003). Indeed, evidence is emerging that species might be able to occupy different niches in their introduced range (e.g. Broennimann *et al.*, 2007).

The results of our study also suggest that rainfall regimes may have an important influence on invasion patterns along an altitudinal gradient. While low precipitation appeared to affect recruitment rather weakly at low to mid-altitudes in the introduced range, the growth and development of established plants of all but one species suffered apparently from the low water availability. These relationships suggest that changed rainfall regimes due to climate change (Christensen *et al.*, 2007) might have a considerable, state- and position-specific effect on the invasion process of an alien plant species along an altitudinal gradient. In our study system, the Wallowa Mountains, increased rainfall might not have a strong positive effect on seedling recruitment except for the lowest (driest) part of the altitudinal gradient. However, development of established plants might benefit strongly from such a changed rainfall regime from low to mid-altitudes, probably leading to quicker and higher reproduction and hence increasing the invasion in this part of the altitudinal gradient. However, not all species might profit from increased rainfall; *Lactuca serriola*, for example, seems to be more adapted to dry soil conditions and is unlikely to profit as much from higher moisture.

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REFERENCES

Alexander, J.M. (2007) Patterns of distributions and traits of Asteraceae forbs along altitudinal gradients in their native and introduced ranges. PhD Thesis. Swiss Federal Institute of Technology (ETH), No. 17399.

Alt, D. & Hyndman, D. (1978) *Roadside geology of Oregon*. Mountain Press Publishing Company, Missoula, Montana.

Antonovics, J. (1976) The nature of limits to natural selection. *Annals of the Missouri Botanical Garden*, **63**, 224–247.

Baker, H. (1965) Characteristics and modes of origins of weeds. *The genetics of colonizing species* (ed. by H. Baker and C. Ledyard Stebbins), pp. 147–172. Academic Press, New York and London.

Baskin, J. & Baskin, C. (1989) Physiological of dormancy and germination in relation to seed bank ecology. *Ecology of soil seed banks* (ed. by M. Leck, V. Parker and R. Simpson). Academic Press, San Diego, California.

Becker, T., Dietz, H., Billeter, R., Buschmann, H. & Edwards, P. (2005) Altitudinal distribution of alien plant species in the Swiss Alps. *Perspectives in Plant Ecology, Evolution and Systematics*, **7**, 173–183.

Broennimann, O., Treier, U., Müller-Schärer, H., Thuiller, W., Peterson, A. & Guisan, A. (2007) Evidence of climatic niche shift during biological invasion. *Ecology Letters*, **10**, 701–709.

Callaway, R. & Walker, L. (1997) Competition and facilitation: a synthetic approach to interactions in plant communities. *Ecology*, **78**, 1958–1965.

Callaway, R., Brooker, R., Choler, P., Kikvidze, Z., Lortie, C., Michalet, R., Paolini, L., Pugnaire, F., Kikodze, D. & Cook, B. (2002) Positive interactions among alpine plants increase with stress. *Nature*, **417**, 844–848.

Cavieres, L., Quiroz, C., Molina-Montenegro, M., Munoz, A. & Pauchard, A. (2005) Nurse effect of the native cushion plant *Azorella monantha* on the invasive non-native *Taraxacum officinale* in the high-Andes of central Chile. *Perspectives in Plant Ecology, Evolution and Systematics*, **7**, 217–226.

Choler, P., Michalet, R. & Callaway, R. (2001) Facilitation and competition on gradients in alpine plant communities. *Ecology*, **82**, 3295–3308.

Christensen, J.H., Hewitson, B., Busuioc, A., Chen, A., Gao, X., Held, I., Jones, R., Kolli, R.K., Kwon, W.-T., Laprise, R., Rueda, V.M.A., Mearns, L., Menéndez, C.G., Räisänen, J., Rinke, A., Sarr, A. & Whetton, P. (2007) Regional climate projections. *Climate change 2007: the physical science basis. Contribution of Working Group I to the Fourth Assessment Report of the Intergovernmental Panel on Climate Change* (ed. by S. Solomon, D. Qin, M. Manning, Z. Chen, M. Marquis, K. B. Averyt, M. Tignor & H. L. Miller). Cambridge University Press, Cambridge, UK, and New York.

Dietz, H. & Edwards, P. (2006) Recognition that causal processes change during plant invasion helps explain conflicts in evidence. *Ecology*, **87**, 1359–1367.

Hügin, G. (1995) Höhengrenzen von Ruderal-und Segmentalpflanzen in den Alpen. *Flora*, **190**, 169–188.

Kitayama, K. & Mueller-Dombois, D. (1995) Biological invasion on an oceanic island mountain: do alien plant species have wider ecological ranges than native species? *Journal of Vegetation Science*, **6**, 667–674.

Kollmann, J. & Banuelos, M. (2004) Latitudinal trends in growth and phenology of the invasive alien plant *Impatiens glandulifera* (Balsaminaceae). *Diversity and Distributions*, **10**, 377–385.

Körner, C. (1999) *Alpine plant life*. Springer, Heidelberg.

Landolt, E. (2003) *Unsere Alpenflora*. Verlag des SAC, Bern.

Maron, J., Vilà, M., Bommarco, R., Elmendorf, S. & Beardsley, P. (2004) Rapid evolution of an invasive plant. *Ecological Monographs*, **74**, 261–280.

Müller-Schärer, H. & Steinger, T. (2004) Predicting evolutionary change in invasive, exotic plants and its consequences for plant-herbivore interactions. *Genetics, evolution and biological control* (ed. by L. Ehler, R. Sforza and T. Mateille), pp. 137–162. CABI Publishing, Wallingford, UK.

Müller-Schärer, H., Schaffner, U. & Steinger, T. (2004) Evolution in invasive plants: implications for biological control. *Trends in Ecology and Evolution*, **19**, 417–422.

Paiaro, V., Mangeaud, A. & Pucheta, E. (2007) Alien seedling recruitment as a response to altitude and soil disturbance in the mountain grasslands of Argentina. *Plant Ecology*, **193**, 279–291.

Parker, I., Rodriguez, J. & Loik, M. (2003) An evolutionary approach to understanding the biology of invasions: local adaptation and general-purpose genotypes in the weed *Verbascum thapsus*. *Conservation Biology*, **17**, 59–72.

Parks, C., Radosevich, S., Endress, B., Naylor, B., Anzinger, D., Rew, L., Maxwell, B. & Dwire, K. (2005) Natural and land-use history of the Northwest mountain ecoregions (USA) in relation to patterns of plant invasions. *Perspectives in Plant Ecology, Evolution and Systematics*, **7**, 137–158.

Parmesan, C. (2006) Ecological and evolutionary responses to recent climate change. *Annual Review of Ecology, Evolution, and Systematics*, **37**, 637–669.

Peterson, A. (2003) Predicting the geography of species' invasion via ecological niche modeling. *The Quarterly Review of Biology*, **78**, 419–433.

Pohs, K. (2000) *The Wallowa Mountains: a natural history guide*. Northwest Mountain Works, Portland, Oregon.

Pugnaire, F. & Luque, M. (2001) Changes in plant interactions along a gradient of environmental stress. *Oikos*, **93**, 42–49.

Rice, K. & Mack, R. (1991) Ecological genetics of *Bromus tectorum*. 3. The demography of reciprocally sown populations. *Oecologia*, **88**, 91–101.

Sakai, A., Allendorf, F., Holt, J., Lodge, D., Molofsky, J., With, K., Baughman, S., McCauley, D., O'Neil, P., Parker, I., Thompson, J.

& Weller, S. (2001) The population biology of invasive species. *Annnual Review of Ecology and Systematics*, **32**, 305–332.

Semple, J. & Cook, R. (2006) *Solidago canadensis. Flora of North America North of Mexico*. (ed. by Flora of North America Editorial Committee, 1993+). 12+ vols., pp. 151–157. New York and Oxford.

Toms, J. & Lesperance, M. (2003) Piecewise regression: a tool for identifying ecological thresholds. *Ecology*, **84**, 2034–2041.

USDA (2007) *The PLANTS database*. (http://plants.usda.gov, 16 March 2007). National Plant Data Center, Baton Rouge, Louisiana.

Weber, E. & Schmid, B. (1998) Latitudinal population differentiation in two species of *Solidago* (Asteraceae) introduced into Europe. *American Journal of Botany*, **85**, 1110–1121.

Werner, P. (1994) *Die Flora*. Verlag Pillet, Martigny, Switzerland.

Wester, L. & Juvik, J. (1983) Roadside plant communities on Mauna Loa, Hawaii. *Journal of Biogeography*, **10**, 307–316.

Williams, D., Mack, R. & Black, R. (1995) Ecophysiology of introduced *Pennisetum setaceum* on Hawaii: the role of phenotypic plasticity. *Ecology*, **76**, 1569–1580.

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